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Spatial mismatch in fish and coral loss following 2016 mass coral bleaching

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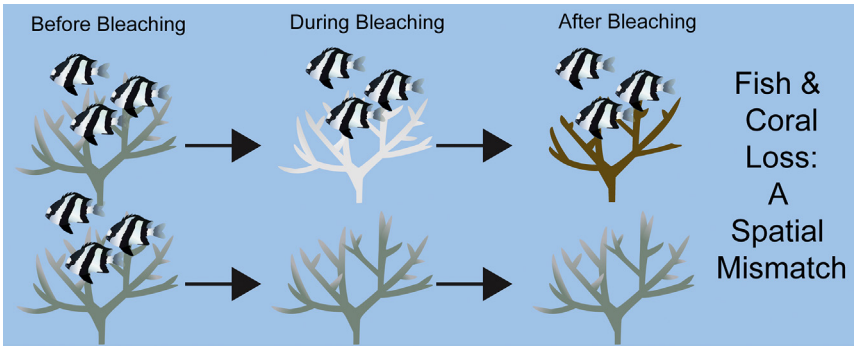
HIGHLIGHTS

- In 2016, the Great Barrier Reef experienced unprecedented mass bleaching of corals.
- At Lizard Island, *Acropora* corals decreased by >95% six months post-bleaching.
- Comparatively, fish losses in coral-associated damselfishes were minor (37%).
- Our novel sampling method revealed a strong spatial mismatch in fish-coral loss.
- Local increases in fish abundance may be indicative of fish spatial movements.

GRAPHICAL ABSTRACT



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ABSTRACT

Record-breaking temperatures between 2015 and 2016 led to unprecedented pan-tropical bleaching of scleractinian corals. On the Great Barrier Reef (GBR), the effects were most pronounced in the remote, northern region, where over 90% of reefs exhibited bleaching. Mass bleaching that results in widespread coral mortality represents a major disturbance event for reef organisms, including reef fishes. Using 133 replicate 1 m^2 quadrats, we quantified short-term changes in coral communities and spatially associated reef fish assemblages, at Lizard Island, Australia, in response to the 2016 mass bleaching event. Quadrats were spatially matched, permitting repeated sampling of fish and corals in the same areas: before, during and 6 months after mass bleaching. As expected, we documented a significant decrease in live coral cover. Subsequent decreases in fish abundance were primarily driven by coral-associated damselfishes. However, these losses, were relatively minor (37% decrease), especially compared to the magnitude of *Acropora* loss (>95% relative decrease). Furthermore, at a local, 1 m^2 scale, we documented a strong spatial mismatch between fish and coral loss. Post-bleaching fish losses were not highest in quadrats that experienced the greatest loss of live coral. Nor were fish losses associated with a proliferation of cyanobacteria. Several sites did, however, exhibit increases in fish abundance suggesting substantial spatial movements. These results challenge common assumptions and emphasize the need for caution when ascribing causality to observed patterns of fish loss at larger spatial scales. Our results highlight the potential for short-term resilience to climate change, in fishes, through local migration and habitat plasticity.

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1. Introduction

Climate change is widely regarded as the greatest threat to the persistence of coral reefs worldwide (Carpenter et al., 2008; Hoegh-

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Guldberg et al., 2007; Hughes et al., 2003, 2018a). Rising ocean temperatures are associated with stronger tropical storms (Knutson et al., 2010; Walsh and Ryan, 2000), infectious coral disease outbreaks (Bruno et al., 2007; Harvell et al., 1999) and most importantly, devastating episodes of mass coral bleaching (Hughes et al., 2017, 2018a). Bleaching occurs when the thermal limits of corals are exceeded and the symbiotic relationship with photosynthetic zooxanthellae (*Symbiodinium* spp.) is disrupted, causing corals to lose colour and become physiologically damaged (Glynn, 1993; Heron et al., 2016; Hoegh-Guldberg, 1999). Although corals are capable of surviving such events, prolonged bleaching often leads to widespread coral mortality (Hoegh-Guldberg, 1999; Hughes et al., 2018b). Over the past two decades, anomalies in sea-surface temperatures have led to three major global bleaching events (e.g. Heron et al., 2016; Hughes et al., 2017, 2018a). This includes the unprecedented mass bleaching of Australia's Great Barrier Reef (GBR) in 2016, which severely impacted over 90% of the reefs in the remote, northern region (Hughes et al., 2017, 2018b).

Coral taxa often show differential responses in their vulnerability to thermal stress. While *Turbinaria* and *Porites* spp. are generally more resistant, branching pocilloporids and acroporids are highly susceptible to bleaching and often experience high levels of mortality (Baird and Marshall, 2002; Hoogenboom et al., 2017; Hughes et al., 2018b; Loya et al., 2001; Marshall and Baird, 2000). Branching species, including *Acropora* species, play a key ecosystem role for many reef fishes, providing both food and shelter (Coker et al., 2013; Pratchett et al., 2008a), and most importantly, increasing the complexity (e.g. rugosity) of coral reefs – an essential component in structuring reef fish assemblages (Graham et al., 2006; Graham and Nash, 2013; Wilson et al., 2008). Hence, widespread loss of branching corals is often tightly linked to significant decreases in reef fish abundance, particularly for small, coral-associated damselfishes and obligate coral-feeding butterflyfishes (Graham et al., 2006; Pratchett et al., 2008a; Wilson et al., 2006). Coral mortality, in general, has also been associated with a decline of non-coral dependent reef fishes (Jones et al., 2004; Pratchett et al., 2011), including planktivorous damselfishes (Booth and Beretta, 2002; Wilson et al., 2006) and various invertebrate-feeding fishes (Wilson et al., 2006), while herbivores and piscivores may increase in abundance following coral bleaching (Garpe et al., 2006; Sheppard et al., 2002; Wilson et al., 2008). These patterns, however, may vary according to the geographic location, temporal scale (i.e. duration since coral bleaching) and subsequent physical and biological disturbances (e.g. tropical cyclones, crown-of-thorns starfish (CoTS) outbreaks), which may further erode coral skeletons and reduce structural complexity (Pratchett et al., 2008a).

Although the effects of coral bleaching on reef fishes have been well documented (reviewed in Hoey et al., 2016; Pratchett et al., 2008a, 2008b, 2011, 2018; Richardson et al., 2018; Wilson et al., 2006), studies to-date have been constrained by the lack of direct spatial-temporal overlap in their sampling design. For example, the majority of studies assess correlative declines before and after a mass bleaching event in the cover of live scleractinian coral (usually along 10 m point intercept transects) and the abundance of various fish species at a substantially larger transect level (100 to 250 m^2 belt transects) (for a discussion of the importance of scale in coral reef fish studies see Yeager et al. (2017)). Although the general assumption is that a loss of live coral, especially habitat-forming *Acropora* species, results in a proportional net loss of coral-dependent reef fishes, no studies, to the best of our knowledge, have explicitly tracked host corals through a mass bleaching event and quantified the changes in the associated reef fish assemblage. Hence, the direct impact of individual coral bleaching, and subsequent mortality, on its 'resident' or closely associated reef fish assemblages, is still largely unknown.

Our study employs a new methodology to explicitly test the assumption that coral mortality leads to the loss of resident fishes. Using replicate 1 m^2 quadrats, we quantified short-term changes in the benthic communities and associated reef fish assemblages, across the ~10 km^2 reefal system of Lizard Island, northern GBR, in response to the 2016 mass coral bleaching event. Importantly, all quadrats were spatially and temporally matched, in that, for each individual quadrat: 1) both benthic and fish taxa were recorded at the same time and at the same spatial scale, and 2) the original quadrat location was clearly identified and was, therefore, able to be reassessed over the course of the bleaching event. Hence, using this sampling design, we were also able to directly test for the strength of the spatial match in coral and fish loss, particularly in coral-associated fishes with small home ranges, following a major bleaching event. We also examined the short-term (6-month) consequences of acute post-bleach cyanobacterial outbreaks. We hypothesized that 1) host coral mortality would lead to a proportional (if non-linear) decrease in the abundance of coral-dependent reef fishes, with a lesser effect on other species, and 2) that fish mortality would be exacerbated by outbreaks of cyanobacteria.

2. Materials and methods

2.1. Study site and timeline of the bleaching event

Our study was conducted at Lizard Island, on the mid-continental shelf, in the northern region of the GBR, Queensland, Australia (14°40′ S, 145°28′E) (Fig. S1 in the Electronic Supplementary Material, ESM). Lizard Island is situated within a marine park and experiences limited fishing pressure; yet surrounding reefs have recently suffered significant environmental damage as a result of ongoing CoTS outbreaks and consecutive tropical cyclones (i.e. 2014, 2015). Between February and April of 2016, Lizard Island and the northern reefs of the GBR experienced prolonged elevated sea-surface temperatures (mean range: 27.1–29.1 °C; Australian Government Bureau of Meteorology, 2016), leading to a devastating mass coral bleaching event across the northern 1000 km of the GBR (Hughes et al., 2017). In order to document temporal changes in both benthic communities and fish assemblages, we collected a series of 'photoquadrats' in 1) January–February 2016, i.e. prior to the bleaching event, 2) April 2016, i.e. during peak bleaching, and 3) October 2016, i.e. 6 months post-bleaching.

2.2. Transects and photographs

We surveyed a total of 19 sites across Lizard Island, which were haphazardly chosen, based on the availability of a reef crest (ESM Fig. S1). Within each site, we swam a transect along the reef 'crest' (at 0–4 m below chart-datum). The reef 'crest' was chosen as it is typically the most dynamic habitat in regards to relative rates of reef processes (Bellwood et al., 2018) and often has the highest coral cover (Wismer et al., 2009). Photographs of a 1 m^2 quadrat (Camera: Nikon Coolpix AW130) were taken at approximately 5 m intervals. Each replicate quadrat consisted of three images: 1) a photograph of the reef and reef fishes (from a distance of approximately 2 m), from a horizontal perspective, i.e. undisturbed and prior to the placement of the quadrat (care was taken to ensure all fishes up to 1.5 m in the water column were included in the photographs, however, in most cases fish were in close proximity to the substratum), 2) a photograph with the 1 m^2 quadrat in place, using the identical camera placement as in the first image, and 3) a planar 'bird's-eye' view of the 1 m^2 quadrat in place on the substratum (Fig. 1). Transects varied in length (range: 50–210 m) and contained between 12 and 38 quadrats. The precise 'starting' location of each transect was identified using GPS coordinates. Subsequently, quadrat locations were relocated using a second underwater camera containing all previous images for reference, repeating the three photographs of the same 1 m^2 area, across all three sampling periods, i.e. before, during and after coral bleaching. All transects were conducted on SCUBA by two divers between 09:00 and 16:00 h.

Our sampling method was specifically designed to minimise the 'diver effect' on fish communities and maximise accuracy of counts on visually apparent small, coral-associated fishes. Standard underwater

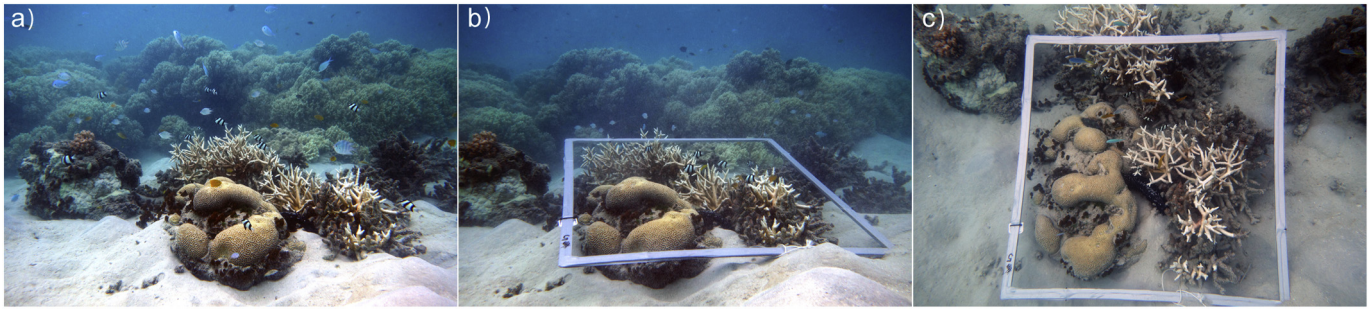

Fig. 1. A photograph series of the same quadrat following our sampling methodology. Photographs a), b) and c) were taken during January–February 2016. Photograph a) was used to quantify the fish community prior to quadrat placement using b) to delineate the area for fish quantification, while c) was taken from a 'birds-eye' view to quantify the benthic covering. Further examples of temporal replicates are provided in the ESM (Fig. S3).

visual census (UVC) techniques of quantifying fish assemblages, especially point censuses or transects where the tape is laid first, can significantly underestimate the abundance of larger vagile fishes by (50 to 70%) through diver disturbance (Dickens et al., 2011; Emslie et al., 2018). They also miss most small, cryptobenthic, fishes (<50 mm) and rely on estimations once large schools of fishes are encountered (Ackerman and Bellwood, 2000). In contrast, our images were taken within seconds of arriving at a site, thus minimising the diver effect and ongoing disturbance. This approach is also relatively insensitive to low visibility or on-going disturbance and can yield precise counts of small fishes rather than estimates of fish schools (it takes up to 30 min to count all fish in one image (maximum 128 individuals)). The method is thus specifically designed to yield replicate, high-resolution counts of small, visually-apparent coral-associated reef fishes.

2.3. Analysis of photographs

A total of 133 (of 451) photoquadrats were analysed. Quadrats were only included if they had a minimum live coral cover of 20% in the first sampling period, as we were explicitly examining coral-fish linkages (coral is used in the broad sense to describe taxa in the orders: Alcyonacea, Corallimorpharia, Helioporacea, Scleractinia; class: Hydrozoa (*Millepora* spp.); (Veron, 2000)). See ESM Text S1 for further details on quadrat selection.

To quantify the abundance and diversity of reef fishes, images were processed in Adobe Illustrator, by drawing an outline of the quadrat on the first, undisturbed photograph, using the second image in the series as a reference. All visible fishes within the delineated 1 m^2 area on the first photograph, and the 1.5 m water column directly above the quadrat (using the quadrat as a guide), were recorded to species level (see ESM Fig. S2). To avoid misidentification of visually similar species, *Chromis viridis* and *C. atripectoralis* were grouped into one species category, '*C. viridis*'. To exclude the effects of recruitment pulses during the summer months, analyses are based on adult fishes only (based on the loss of juvenile colouration and or being over approximately 25% of the maximum adult size).

The benthic community was quantified using the third, i.e. planar, image (see ESM Fig. S3) and processed using the software photoQuad (Trygonis and Sini, 2012), which generates stratified randomized points (n = 40) over the photoquadrat. Under each point the benthic covering was recorded. For corals, the genus, growth form and bleaching status were recorded. Only corals and cyanobacteria cover are considered herein and relative benthic cover of these categories was based on the 40 points. Only 10 of the 15,960 benthic points examined were categorized as 'unidentifiable' and were excluded from subsequent analyses. For graphical purposes, the relative level of coral cover remaining during and after bleaching was calculated individually in each plot by calculating cover remaining as a percentage of the initial (100%) cover. To assess the effect of random sampling and variation in quadrat placement, 15 randomly selected 'after' quadrats were examined using the 40 random points vs the exact same 40 points as used in the 'before' quadrat. With a mean difference of just 1.4% our repeat quadrat method was found to provide a good indication of benthic changes among temporal samples (see ESM text S2, ESM Table S1 for full details).

2.4. Data analysis

We used generalized linear mixed effects models (GLMMs) to test for differences in the proportional cover of live coral, soft coral, *Acropora* spp. and scleractinian corals, as well as fish abundance and fish species richness, among the three sampling periods, i.e. before, during and after mass bleaching. Fish abundance data were examined using a GLMM with a negative binomial distribution, to account for the non-normal and overdispersed nature of the count data, while fish species richness data were examined using a GLMM with a Poisson distribution, suitable for count data which is not overdispersed. Coral cover data were examined using GLMMs with binomial distributions in all cases. Where overdispersion was present in the binomial models, an observation-level random effect was employed to account for this. In all models, sampling period (before, during, after mass bleaching) was fitted as a fixed effect, while quadrat ID nested within transect ID were fitted as random effects. The random effects accounted for the lack of spatial independence and the repeated measures sampling design. Model fits were evaluated using residual plots. Statistical modelling was performed in the software R (R Core Team, 2017), using the lme4 (Bates et al., 2015) package.

Changes in the assemblages of corals (genera) and reef fishes (species) were first examined using non-metric multi-dimensional scaling (nMDS) ordinations. Ordinations were based on zero-adjusted Bray Curtis similarity matrices of square root transformed coral cover and fish abundance data to decrease the impact of highly abundant taxa. Differences between groups in the ordinations were tested using permutational multivariate analysis of variance (PERMANOVAs). In the PERMANOVA design, sampling time was treated as a fixed factor, while quadrat ID nested within transect ID were treated as random factors to account for the repeated measures design and the lack of spatial independence. Following the PERMANOVAs, pair-wise tests were performed to examine within-factor differences. Assumptions of homogeneity of dispersions were tested using permutational analysis of multivariate dispersions (PERMDISPs). Canonical analysis of principle coordinates (CAP) was then used to explore specific differences among sampling periods (before, during, and after mass bleaching) identified in the PERMANOVAs.

A non-parametric distance-based linear model (DISTLM) was used to examine the relationship between changes in the fish assemblage (at a species level) with the changing coral assemblage (genus level). Based on a multiple regression model, the DISTLM examines the relationship between the fish assemblage data and coral assemblage data

to find the combination of coral genera that explains the greatest variation in the fish assemblage data. The initial model fitted all coral genera and then a backwards selection routine based on Akaike's Information Criterion (AIC) was employed to select the most parsimonious model of coral genera that explained changes in the fish assemblage (ESM Table S2). Distance-based redundancy analysis (dbRDA) was then used to visualise the most suitable model. Multi-collinearity was initially assessed using draftsman plots. All multivariate analyses were performed using PRIMER 7.0 PERMANOVA+.

In addition to the DISTLM, we also explicitly examined relationships between certain benthic categories and fish loss. Specifically, linear regressions were used to examine the relationship between changes in the cover of *Acropora*, scleractinian corals, structurally complex corals, combined 'total' corals and soft coral, with changes in fish abundance, i.e. before vs. after bleaching. Additionally, we examined the relationship between 1) cyanobacteria cover during bleaching and fish loss (before vs. after bleaching), and 2) the relationships between the cover of bleached *Acropora*, soft corals and scleractinian corals with fish loss (before vs. during bleaching). Fits of linear regressions were assessed with residual plots. All statistical analyses were conducted on absolute data. Data standardised to a relative scale were only used for graphical purposes.

3. Results

3.1. Changes in coral cover, reef fish abundance and reef fish species richness

The percent cover of live coral decreased significantly over time (Fig. 2a). Compared to images prior to bleaching, total live coral cover was significantly lower both during (GLMM; $P \leq 0.001$) and after (GLMM; $P \leq 0.001$) mass bleaching, with relative decreases of 36.7 and 44.7% from pre-bleaching levels, respectively (Fig. 2a; ESM Tables S3, S4). The impact of bleaching was most pronounced for soft corals (Order Alcyonacea) and *Acropora* (Order Scleractinia) (Fig. 2a). Six months post-bleaching, the relative cover of soft coral and *Acropora*, on average, decreased by 69.5 and 96.4% from initial levels, respectively (Fig. 2a). Other scleractinian corals, excluding *Acropora* species, also decreased significantly, both during (GLMM; $P < 0.001$) and after (GLMM; $P < 0.001$) bleaching, with a total relative decline of 11.1% (ESM Fig. S4;

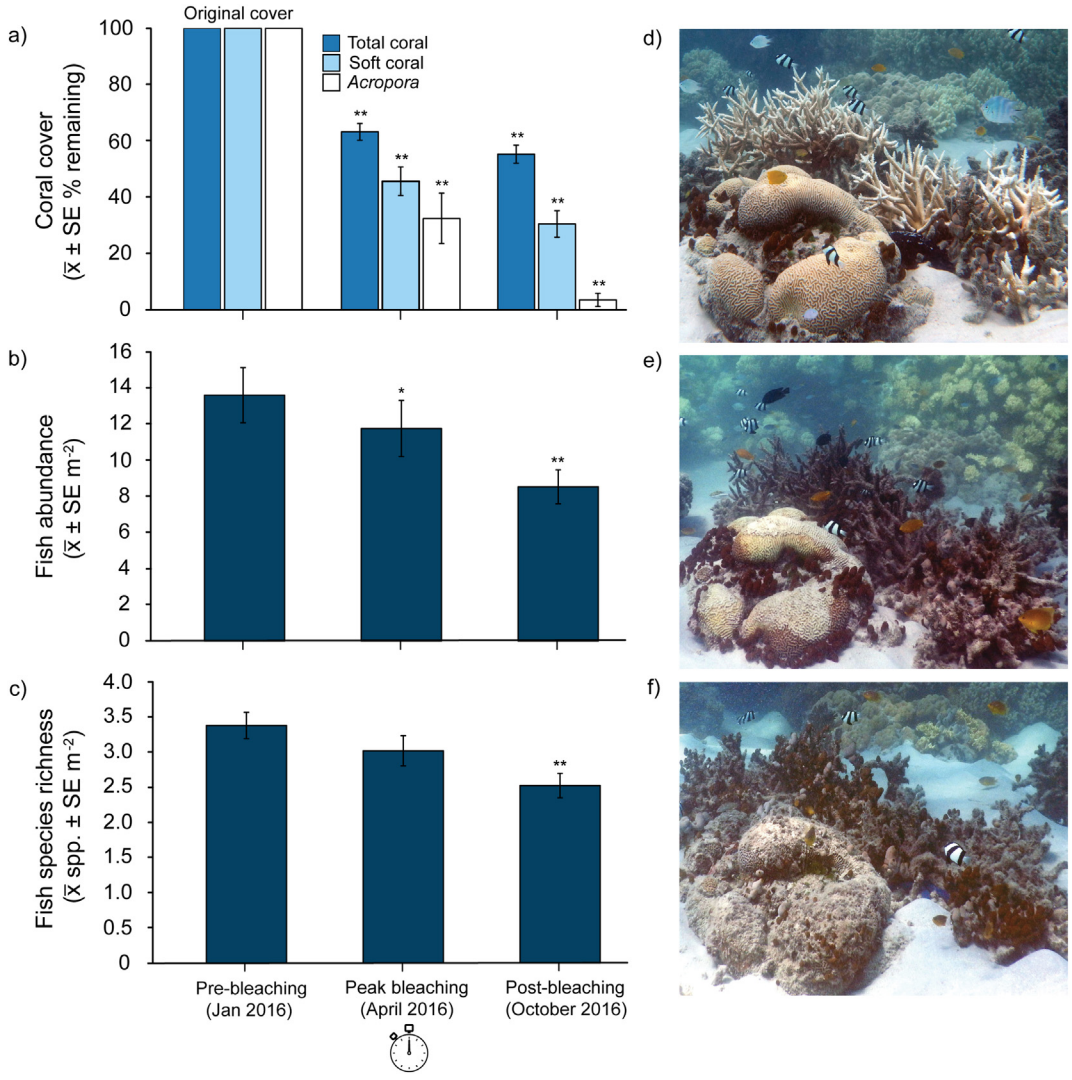

Fig. 2. Temporal variation in live coral cover and reef fishes following mass coral bleaching at Lizard Island, Australia. Changes in a) coral cover, b) fish abundance and c) fish species richness, sampled before, during and after mass bleaching. Total coral includes all nominal coral-like taxa (orders: Scleractinia, Helioporacea, Alcyonacea, Corallimorpharia; class: Hydrozoa - *Millepora* spp.), presented as relative cover (i.e. percent cover remaining of the original cover). Fish values represent absolute values. Asterisks represent significant differences in comparison to the first sampling period, ** = $P < 0.001$, * = $P < 0.05$. Fish and coral changes d) before, e) during and f) after coral bleaching. Note the complete loss of *Acropora* but the coral-associated *Dascyllus aruanus* remain.

ESM Tables S3, S4). Absolute values (mean ± SE; range) for changes in the cover of various coral categories are provided in ESM Table S5.

In general, reef fishes followed a similar pattern to corals, in that fish abundance decreased significantly over time, with fewer individuals recorded during (GLMM; $P \leq 0.01$) and after (GLMM; $P \leq 0.001$) mass bleaching, compared to initial images (Fig. 2b; ESM Tables S3, S4). Absolute values (mean ± SE; range) for changes in the abundance of total fishes and focal damselfishes are provided in ESM Table S6. Although species richness did not decrease significantly between before and during samples (GLMM; $P = 0.096$), there were fewer fish species recorded post-bleaching (GLMM; $P < 0.001$) (Fig. 2c; ESM Tables S3, S4).

In total, we documented changes in the abundance of 120 species of reef fishes. Of the species with 5 or more individuals observed (Fig. 3), the majority (76.9%) decreased in abundance in response to bleaching, with three coral-associated damselfishes (*Chromis viridis*, *Pomacentrus moluccensis*, *Neopomacentrus azysron*) accounting for over 54% of total fish loss. These damselfishes lost most individuals (Fig. 3), with relative losses equating to decreases of 38.3, 32.7 and 39.1%, respectively (ESM Fig. S5). Losses of individuals in other species were relatively minor (Fig. 3). Eight species increased in abundance post-bleaching (mean = 7.5 individuals), with most additional individuals in the damselfish *Acanthochromis polyacanthus* (40.4% relative increase) (Fig. 3).

3.2. Community change and interrelationship

The coral community shifted significantly following the bleaching event (PERMANOVA: Pseudo-$F_{2, 398} = 37.499$, $p_{[perm]} = 0.0001$), driven primarily by a near complete loss of *Acropora* (Fig. 4a). Pair-wise tests revealed that the coral assemblage was significantly different, from pre-bleaching conditions, during ($t = 6.003$, $p_{[perm]} = 0.0001$) and after ($t = 7.4394$, $p_{[perm]} = 0.0001$) mass coral bleaching as well as between peak bleaching, compared to post-bleaching ($t = 3.1072$, $p_{[perm]} = 0.0001$). Based on the PERMDISP, there was no significant variation in the coral community dispersion across sampling periods ($F_{2, 396} = 2.2387$, $p_{[perm]} = 0.2159$).

Significant, although less pronounced, shifts in the community assemblage of reef fishes were also documented (PERMANOVA: Pseudo-$F_{2, 398} = 3.5194$, $p_{[perm]} = 0.001$), largely driven by a reduction in small damselfish species (Fig. 4b). Pair-wise tests revealed significant before vs. after bleaching ($t = 2.2597$, $p_{[perm]} = 0.0001$), before vs. during ($t = 1.7029$, $p_{[perm]} = 0.004$) and during vs. after ($t = 1.5118$, $p_{[perm]} = 0.021$) effects. There was no significant variation in fish assemblage dispersion among sampling periods ($F_{2, 396} = 2.9419$, $p_{[perm]} = 0.0826$).

However, the DISTLM revealed that the ability of the coral assemblage to predict the change in the fish assemblage at each site was minimal. The best fit model contained 13 genera of coral, yet only explained 9.97% of the total variation in fish abundance ($R^2 = 0.0997$). Change in *Acropora* was the single best predictor of changes in fish communities, but only explained 1.28% of the total variation in fish composition (ESM Table S7).

Furthermore, based on specific linear regressions, we documented no significant relationships between changes in the abundance of reef fishes and the cover of various benthic categories including *Acropora*, scleractinian corals, structurally complex corals, combined 'total' corals, soft coral, cyanobacteria, bleached *Acropora*, bleached scleractinian corals and bleached soft coral (ESM Figs. S6–11; ESM Tables S8, S9).

3.3. Spatial responses of reef fishes to Acropora loss and cyanobacteria outbreaks

Post-bleaching, live *Acropora* cover decreased in 98% of *Acropora*-containing quadrats (i.e. 53 quadrats decreased in cover). *Acropora* accounted for 2.5 to 80% of the decrease in total cover, with a mean contribution of 16.8% (Fig. 5a). Total reef fish abundance both decreased (n = 86 quadrats, 69.4%) and increased (n = 38 quadrats, 30.6%) in quadrats post-bleaching, ranging from a loss of 67 individuals to an increase of 52 individuals per quadrat (Fig. 5b). Damselfishes likewise showed both marked decreases and increases within individual quadrats (Fig. 5c). However, decreases in the abundance of reef fishes, including damselfishes,

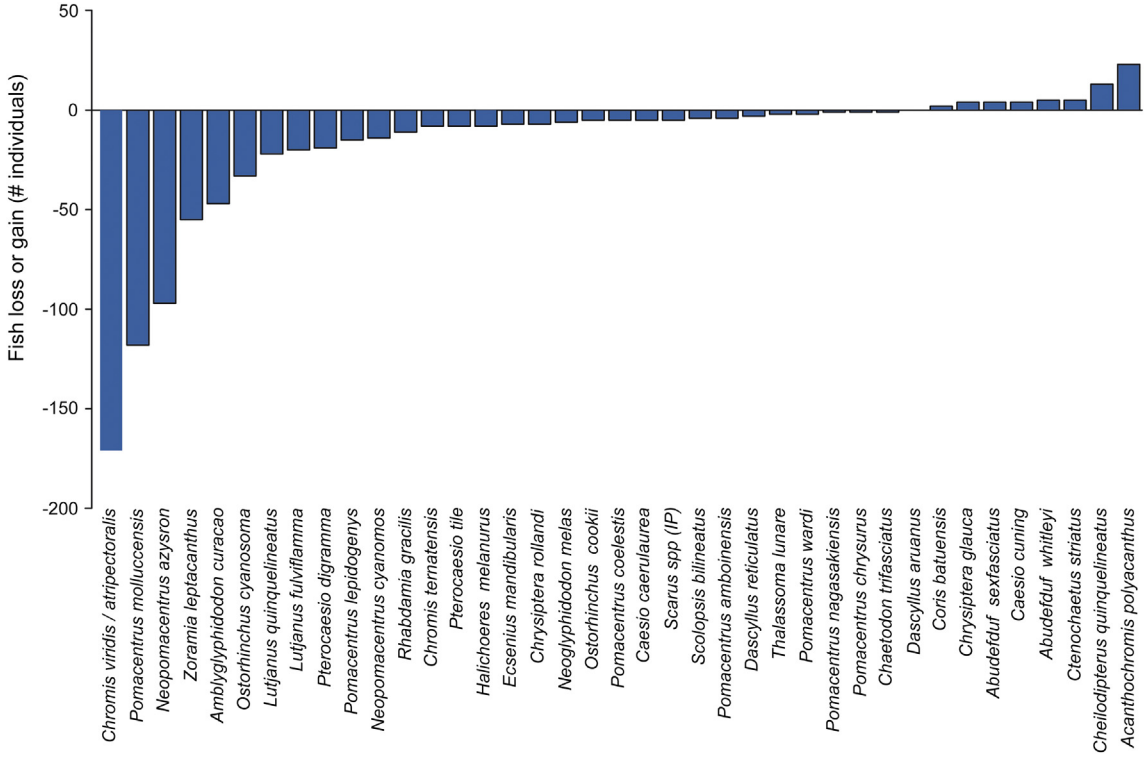

Fig. 3. Response of 39 reef fish species to mass coral bleaching. Values represent total changes in the abundance of each species 6 months post-bleaching (October 2016), compared to the initial sampling period in January 2016 (values based on 133 m^2 of quadrats). Only species with 5 or more individuals are shown.

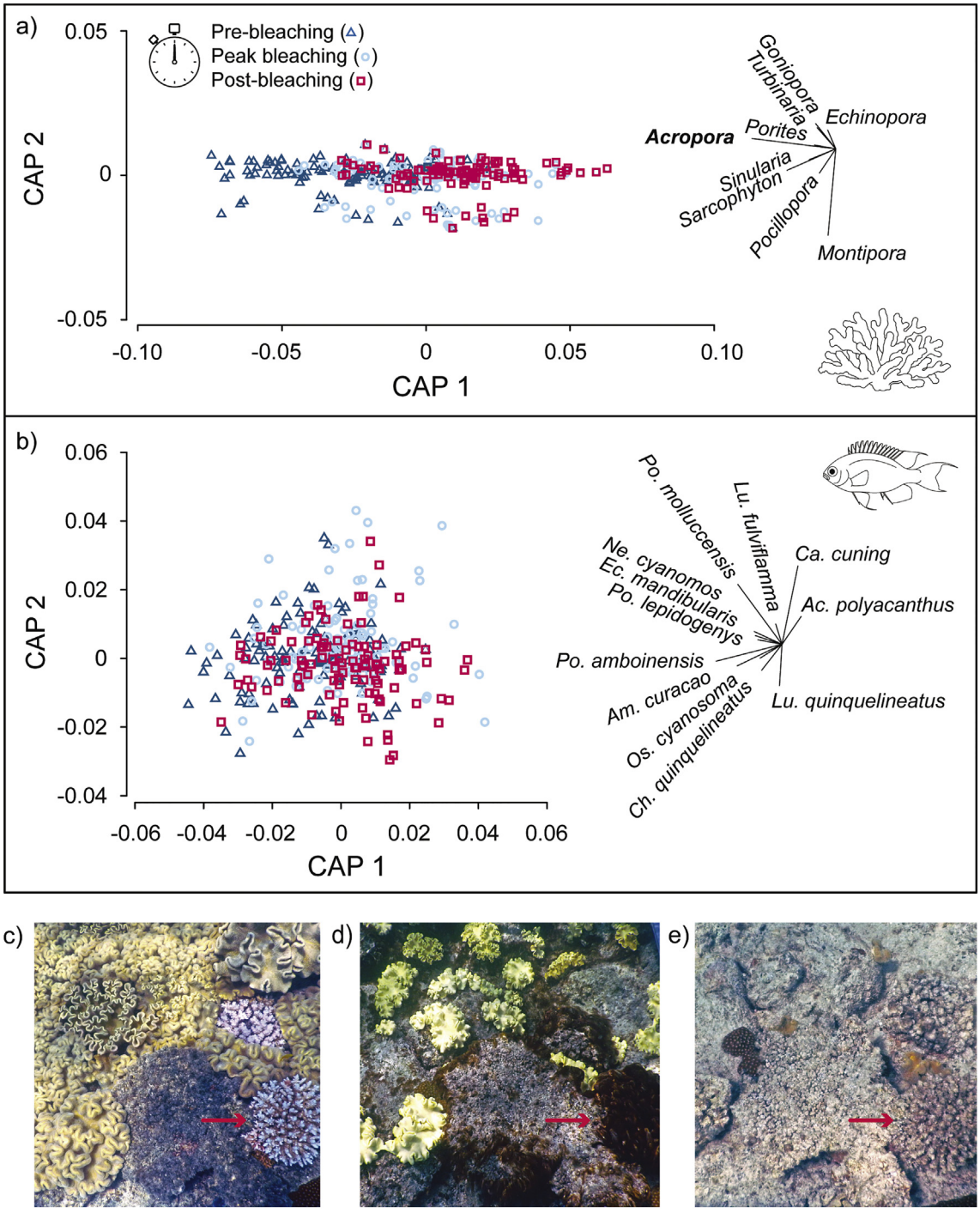

Fig. 4. Coral and fish community change in response to mass bleaching. Canonical Analysis of Principal coordinates (CAP) analysis of a) coral and b) reef fishes, showing shifts in assemblages over time; Coloured symbols represent sampling periods, before (dark blue triangle), during (light blue circle) and after (red square) mass bleaching. Vectors on both CAPs were calculated following a multiple correlation model; only taxa with a correlation coefficient > 0.15 are displayed. Note the dramatic change in coral composition with the loss of *Acropora* and the absence of such a change in fish composition. Photographs show transformation of soft corals (*Sarcophyton*) and corymbose *Acropora* over time: c) pre-bleaching (intact), d) during peak bleaching (bleached; covered in cyanobacteria), and e) post-bleaching (absent; dead). Red arrows highlight changes in an *Acropora* colony over time, from live, smothered by cyanobacteria then covered in turf algae.

were evenly spread across quadrats. They were not concentrated in those quadrats which exhibited the highest loss of *Acropora* (Fig. 5abc). There was no significant relationship between *Acropora* loss and fish loss ($R^2 = 0.0083$, $P = 0.2957$; ESM Fig. S6a; Table S8). This spatial mismatch of coral and fish loss was apparent for all focal coral groups (i.e. total coral, structurally complex corals, scleractinian corals, soft corals and bleached categories) (ESM Figs. S6–S11, ESM Table S8, S9).

A similar pattern was seen in cyanobacteria. During peak bleaching, cyanobacteria outbreaks occurred in 37 quadrats, with a mean percent cover of 23.9% where present (ranging from 2.5 to 97.5% of the quadrat) (Fig. 6a). Again, we recorded both decreases (e.g. post-bleaching n = 86 quadrats, 69.4%) and increases (e.g. post-bleaching n = 38 quadrats, 30.6%) in the abundance of reef fishes within individual quadrats (Fig. 6bc). Yet, across both sampling periods, fish losses were not concentrated in quadrats containing the highest cover of cyanobacteria

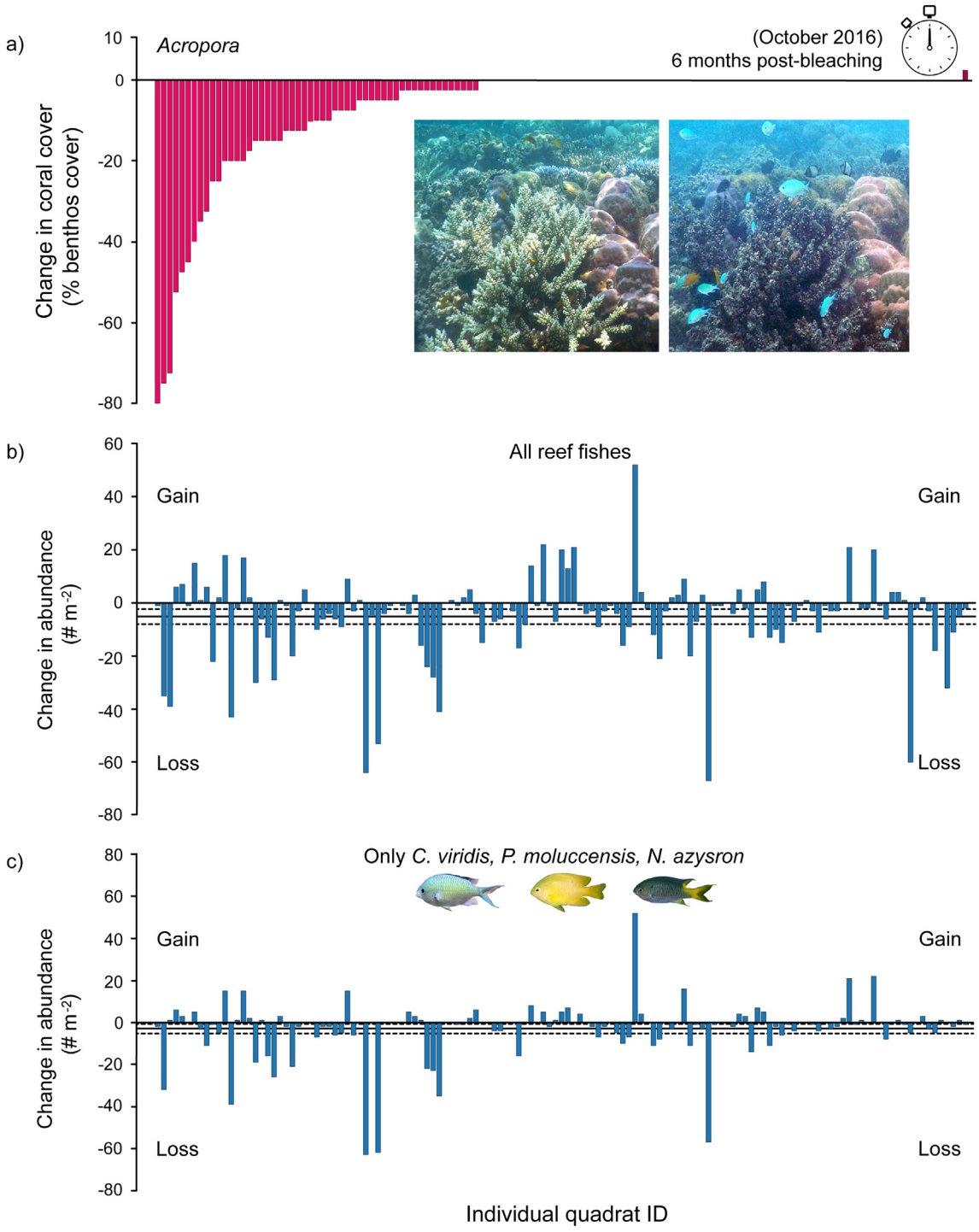

Fig. 5. Spatial mismatch in fish and *Acropora* losses. Changes in a) the percent cover of *Acropora*, b) total fish abundance and c) damselfishes (*Chromis viridis, Pomacentrus moluccensis, Neopomacentrus azysron*) across individual matched quadrats before (January 2016) and after (October 2016) mass bleaching. Dashed lines: 95% confidence interval. Insert photographs show an *Acropora* colony before and after (dead) mass bleaching. Note the fish in the insert photographs, particularly the coral associated *Chromis viridis* in the foreground and *Dascyllus reticulatus* in the background of the after photo.

(Fig. 6abc), again with no significant relationship ($R^2 = 0.0121$, $P = 0.2076$) (ESM Fig. S6f; ESM Table S8).

4. Discussion

4.1. Coral bleaching, Acropora loss and the effects on coral-dwelling reef fishes

Between 2015 and 2016, record-breaking global temperatures caused widespread, pan-tropical bleaching of scleractinian corals (Hughes et al., 2017, 2018a). On the GBR, the effects were most pronounced in the remote, northern region (Hughes et al., 2017, 2018b). Using a series of spatially and temporally matched photoquadrats, we documented the short-term changes in coral and fish communities following mass coral bleaching. In general, corals showed the expected changes in response to thermal stress, i.e. most corals exhibited high levels of bleaching, *Acropora* species showed the highest levels of coral mortality and dead corals were subsequently inundated by cyanobacteria. However, fish loss was not commensurate with the magnitude of coral loss. The relative abundance of fishes decreased by approximately 30%, especially planktivorous coral-dependent

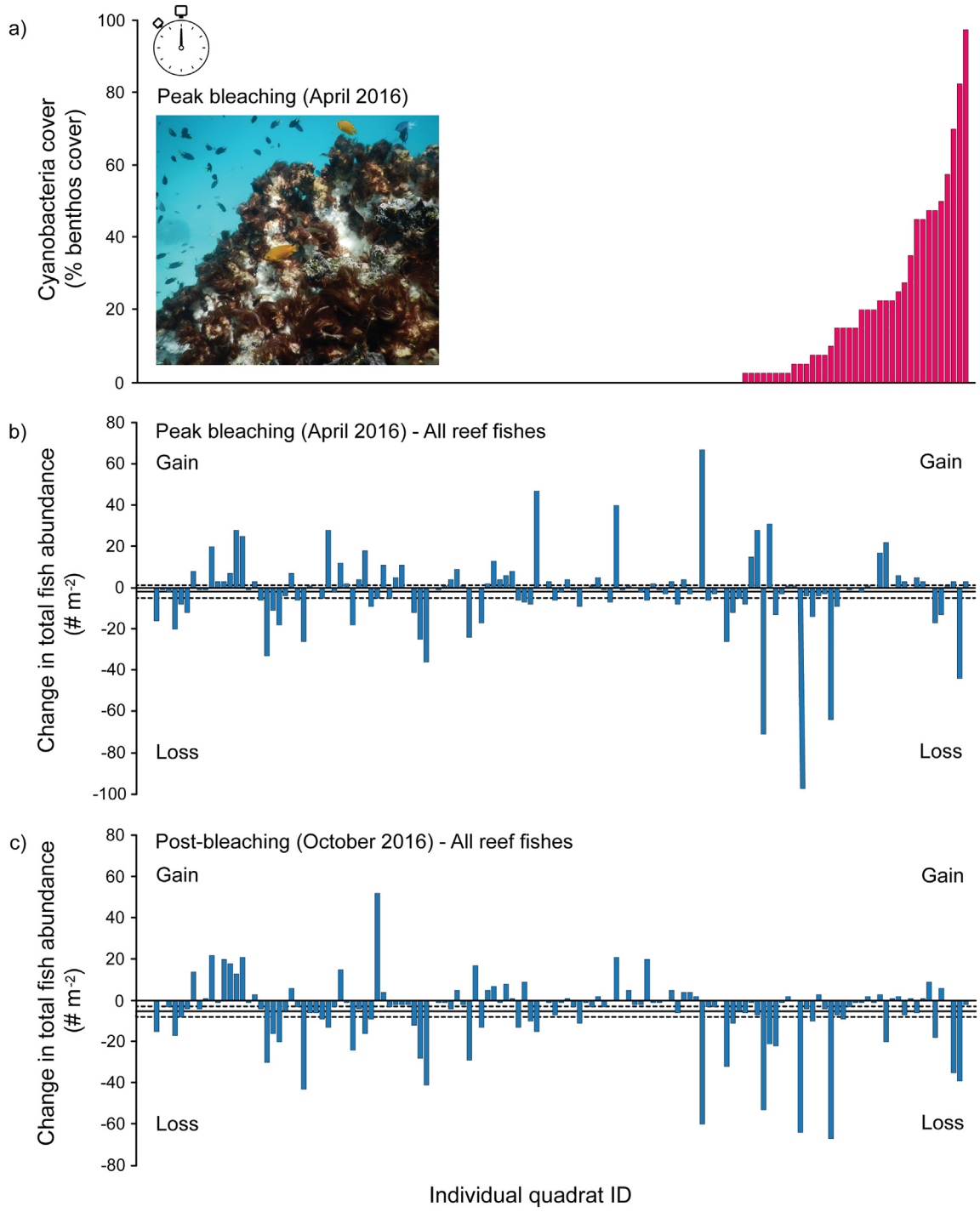

Fig. 6. Spatial mismatch in cyanobacteria and fish losses. a) Percent cover of cyanobacteria across individual matched quadrats, during the second sampling period in April 2016 (peak of bleaching). b) Changes in the abundance of reef fishes within individual quadrats in April 2016 (peak bleaching) and c) in October 2016 (post-bleaching), compared to January 2016 (pre-bleaching). Dashed lines: 95% confidence interval. Insert photograph shows invasion of cyanobacteria on bleached encrusting *Montipora*.

damselfishes. Furthermore, there was no spatial match between coral loss and fish loss. Fishes responded at a reef scale, but not at a local, quadrat scale.

Branching corals play key functional roles on coral reefs (Bellwood et al., 2004), by providing food (Coker et al., 2013) and increasing the structural complexity of reef habitats. This has been identified as a key element in the survival of many species of small-bodied reef fishes (Graham et al., 2006; Wilson et al., 2008). Species that live in close association with branching corals, e.g. damselfishes, often exhibit pronounced decreases in abundance in response to bleaching and or habitat loss, a phenomenon that has been repeatedly documented across multiple spatial scales (e.g. Bellwood et al., 2006; Booth and Beretta, 2002; Ceccarelli et al., 2016; Halford et al., 2004; Jones et al., 2004; Pratchett et al., 2008a; Spalding and Jarvis, 2002; Wilson et al., 2008). Our results support this general pattern, yet they raise questions about our assumptions regarding the basis of this decline.

4.2. Perspectives on a novel sampling methodology

Our novel sampling methodology provides a unique, fine-scale understanding of how coral bleaching, and subsequent mortality, affects reef fishes. Spatially and temporally matched quadrats allowed us to

track specific reef sites over the course of a mass bleaching event, and for the first time, we were able to explore subsequent responses of, as well as, direct interactions between corals and fishes. Our methods are particularly suited for quantifying effects on reef fishes that live and feed in close proximity to corals, by using quadrats that generally approximate the resting home ranges of these small fishes (e.g. Nash et al., 2015). Quantitative data on the home ranges and site fidelity of small coral-associated reef fishes are scarce and limited to few species (but see Bellwood et al., 2016a; Booth, 2016; Gardiner and Jones, 2016; Marnane, 2000; Rueger et al., 2014; Sale, 1971). However, all evidence suggests that these fishes move only centimetres to a few meters, with most exhibiting high site-fidelity and or site attachment (Streit and Bellwood, 2017, 2018). Our method is therefore likely to provide a representative indication of the fishes within the local vicinity. Furthermore, quadrats were extensively replicated across the ~10 km^2 reefal system of Lizard Island, which also allowed us to examine coral – fish interactions at a broader scale.

Importantly, we were able to measure changes in fish abundance and changes in coral cover simultaneously at the same fine spatial scale. This allowed us, for the first time, to assess any local, small-scale correlations. By contrast, previous studies generally use estimates of fish abundance and or coral cover averaged across larger areas (e.g. Booth and Beretta, 2002; Sano, 2004; Shibuno et al., 1999), which provides little information in regards to where post-bleaching decreases were most pronounced (i.e. bleached versus unbleached corals), as data rarely provide a direct spatial overlap between fishes and corals. Moreover, by analysing digital photographs, we had minimal observer-effects (scaring fishes) and were not constrained by time, which ensured that all visible fishes were accounted for (i.e. counting versus estimating). In some cases it took approximately 30 min to analyse a single m^2 quadrat for fishes, delivering a degree of precision that is not available during typical underwater visual census techniques. Fish identification could also be verified by more than one observer. Finally, timing was closely tied to the bleaching event, the first series of photographs were taken in January 2016, directly prior to the world's largest bleaching event, allowing us to document the short-term responses of corals and fishes in naturally occurring communities within a protected reef system.

We do, however, recognize certain methodological limitations. Firstly, quantifying reef fishes from digital photographs is not common practice, as it provides a single 'snapshot' with individuals potentially hidden from view behind physical structures or photographed at an angle which makes identification challenging (although this is common to all visual censuses). Secondly, given the small spatial scale of individual quadrats, there is the potential to underestimate larger more vagile fishes. However, abundance estimates before bleaching of large functionally important (e.g. Acanthuridae: 9.8 indv. 100 m^{-2}), or coral-dependent (e.g. Chaetodontidae: 6.8 indv. 100 m^{-2}) species were comparable to previous estimates from Lizard Island and nearby reef crests using traditional methods, 7.2 and 8.3 indv. 100 m^{-2}, respectively (Bellwood et al., 2018; Pratchett and Berumen, 2008). Furthermore, our sampling design was specifically designed to examine changes in small coral-associated reef fishes that are documented to suffer most from the direct consequences of live coral loss (Booth and Beretta, 2002; Ceccarelli et al., 2016; Graham et al., 2006). Finally, our study was restricted to adult fishes and only investigates short-term (i.e. 6 months after peak bleaching) responses of benthic communities and associated reef fishes. Although there are methodological limitations, this novel sampling technique has the potential to reveal patterns that may remain 'hidden' using traditional methods.

4.3. Spatial mismatch in coral versus fish loss

Overall, changes in fishes were far less pronounced than expected. For example, the abundance of obligate live coral-dwellers (*P. moluccensis* and *C. viridis*) did not decrease in proportion to *Acropora* loss. The relative cover of live *Acropora* decreased by over 95% by the third sampling period, while losses in these fishes only ranged from 32.7 in *P. moluccensis* to 38.3% in *C. viridis*. By contrast, in 1999, Pratchett et al. (2012) documented a 30 and 40% decrease in the abundance of *P. moluccensis* and *C. viridis* at Lizard Island, respectively, in response to a CoTS outbreak that reduced total live coral cover by just 20% (primarily branching acroporids and pocilloporids). Given the staggering loss in *Acropora* cover, we expected far stronger responses in these fishes. It may be that CoTS and bleaching produce different chemical signatures, however, both result in similar algal-covered coral skeletons after 6 months. It was particularly noteworthy that fish losses were limited even when *Acropora* cover was <5% and in many areas 0% cover.

One of our most unexpected findings, however, was the strong spatial mismatch between fish and coral loss. Quadrats depleted of live coral were expected to result in comparable decreases in fish abundance, or at least, to exhibit higher fish losses compared to quadrats less affected by bleaching, particularly for obligate live coral-dwellers. This was not the case. At a quadrat level, the results clearly show that reef fishes, including coral-associated damselfishes, increased in abundance at several sites that experienced a significant loss in the cover of live coral, including *Acropora*. Hence, fishes increased in areas dominated by dead corals 6 months post-bleaching, which supports the notion that fishes are capable of occupying dead corals as long as the underlying skeleton, and hence, structural complexity, remains intact (e.g. Lindahl et al., 2001; Sano, 2004) (see insert in Fig. 5). Similarly, decreases in fish abundance were not restricted to, or focused on, quadrats that exhibited a loss of live coral. Although coral mortality probably played a major role in decreasing the overall abundance of reef fishes post-bleaching, our results are strongly indicative of fish movement. Numerous quadrats across Lizard Island exhibited increases in the abundance of reef fishes post-bleaching. Fishes, therefore, may be vacating degraded habitats, possibly due to increasing intra- and interspecific competition, and moving to alternate reef locations. Such post-disturbance spatial movement patterns have been inferred in several previous studies. For example, in response to storm damage, fishes were thought to vacate shallow, degraded reef habitats in favour of deeper waters (e.g. Letourneur et al., 1993; Walsh, 1983), with subsequent recolonization of shallow habitats when environmental conditions were suitable (Letourneur et al., 1993). Experimental evidence also suggests that some coral-dwelling reef fishes are able to successfully relocate to healthy coral colonies following bleaching and subsequent mortality of their coral host (Coker et al., 2012). Our results suggest that this behaviour may be relatively common at local scales.

An interesting question to consider is at what scale does this spatial mismatch dissipate? However, the answer may be that no such dissipation will occur. Indeed, recent evidence from the GBR, on the 2016 bleaching event, found that changes in the abundance and or richness of coral reef fishes were poorly predicted by the loss of corals at both a system level (Richardson et al., 2018) and a regional level (Stuart-Smith et al., 2018). Our results, both support and extend these previous findings, by revealing that this spatial mismatch between fish loss and coral loss occurs down to a 1 m^2 scale. Evidently, the relationship between coral loss and fish loss may not be as clear-cut as often assumed.

Overall, decreases in fish abundance were probably a result of predation, exacerbated by coral bleaching and competition. Coker et al. (2009) demonstrated that predation on coral-dwelling damselfishes (*P. moluccensis* and *Dascyllus aruanus*) was higher on bleached and recently dead corals, compared to healthy colonies. This may be due to increased visibility of prey in front of a white background and or the absence of stinging nematocysts, which otherwise deter predators on live corals (Coker et al., 2009), especially invertebrate predators (Goatley et al., 2017). Increased predation in such suboptimal reef habitats may also drive fish movement to neighbouring, healthy coral colonies (Coker et al., 2009). Competitive interactions may also exacerbate fish mortality post-bleaching. Both sessile and mobile taxa often compete for space within reef environments (e.g. Bonin et al., 2015; Kerry

and Bellwood, 2016; Lang and Chornesky, 1990; McCook et al., 2001; Webster and Hixon, 2000), and competition may intensify following large scale coral loss when critical resources become limited. Fishes that attempt to relocate to healthy coral colonies may experience increased agonistic interactions from resident fishes (Coker et al., 2012), while dominance hierarchies may be altered (Bonin et al., 2015), and density-dependent mortalities increase in degraded habitats (e.g. Boström-Einarsson et al., 2013; Holbrook and Schmitt, 2002). However, despite these widespread reports, we only documented a 37% decline in small reef fishes while recording a 96% loss of *Acropora*.

This evidence calls for care in our interpretation of the effects of reef degradation on fish loss. At a local, 1 m^2 scale, significant coral loss does not necessarily equate to a proportional, even if not linear, loss of fishes, particularly in the short-term. Our new methodology revealed unprecedented variation in the responses of resident reef fishes to coral loss, showing the widespread ability of fishes to use alternate reef habitats, as well as, strong evidence for habitat shifts. It should be noted that some of this variation may have resulted from repetitive sampling at this small scale through time. However, across individual quadrats, we repeatedly documented increases in the abundance of resident reef fishes in areas that exhibited significant *Acropora* loss. At other locations, we recorded the ability of *C. viridis* to relocate into *Heliopora* corals (F: Helioporidae) that were previously unoccupied (photographs provided in Fig. 7). The ability of these fishes to switch to degraded or alternate corals suggests that the 'need' for live *Acropora*, may be a preference, rather than an obligate requirement. This pattern raises questions regarding the evolution and history of coral-fish associations (Bellwood et al., 2016b). In the Mediterranean, for example, *Chromis chromis*, which is morphologically and functionally similar to *C. viridis*, has no access to, or need for, live branching corals. Instead, they are commonly found over seagrass beds and rocky-algal habitats (Guidetti, 2000; Guidetti et al., 2004). Our study highlights the need to carefully consider the requirement and preferences of coral dwelling species, which exhibited surprisingly flexible habitat associations when faced with significant coral loss.

Labile habitat associations are a key sign of potential resilience to changing reef environments, particularly in species that normally express strong habitat preferences (Streit and Bellwood, 2018). Invasion success of Red Sea species into the Mediterranean, for example, is largely dependent on climatic affinity and ecological traits, that include home range size (Belmaker et al., 2013; Parravicini et al., 2015), where shifts in such traits may permit successful establishment. Success for reef fishes in modern-day, changing reefs may ultimately depend on the ability of fishes to adjust and shift habitat requirements. On coral reefs, obligate corallivores are often most vulnerable to coral loss, particularly species with narrow dietary niche breadths (Pratchett et al., 2006). However, even highly specialized coral-feeding reef fishes may be capable of feeding behaviour that is more flexible than previously assumed (e.g. *Chaetodon trifascialis*) (Lawton et al., 2012), making them potentially less vulnerable to climate change. Furthermore, recent experimental evidence on forced movement and homing behaviour demonstrated that some damselfishes (e.g. *P. moluccensis*) continue to migrate to other sites post-homing, even in species that exhibit strong homing tendencies (Streit and Bellwood, 2017, 2018). In the current study, we show that damselfishes appear to shift from host corals to alternate habitats in response to mass bleaching. The association between coral-dwelling damselfishes and specific host corals or reef sites may be more flexible than previously assumed.

4.4. Cyanobacteria and the response of reef fishes

Dense mats of cyanobacteria are often an ephemeral symptom of recent reef degradation, as dying corals undergo a series of successional changes. These cyanobacterial mats are associated with a range of detrimental effects including the potential to overgrow and smother benthic organisms, including corals (Ford et al., 2018), inhibiting coral recruitment (Kuffner et al., 2006), and increasing coral diseases (Sato et al., 2017). Cyanobacteria also appear to be detrimental to fishes, increasing predation risk (McCormick, 2012; McCormick et al., 2017) and producing toxins considered harmful to reef fishes (Golubic et al., 2010; Leao et al., 2012). Post-bleaching colonization of cyanobacteria is therefore expected to exacerbate fish loss.

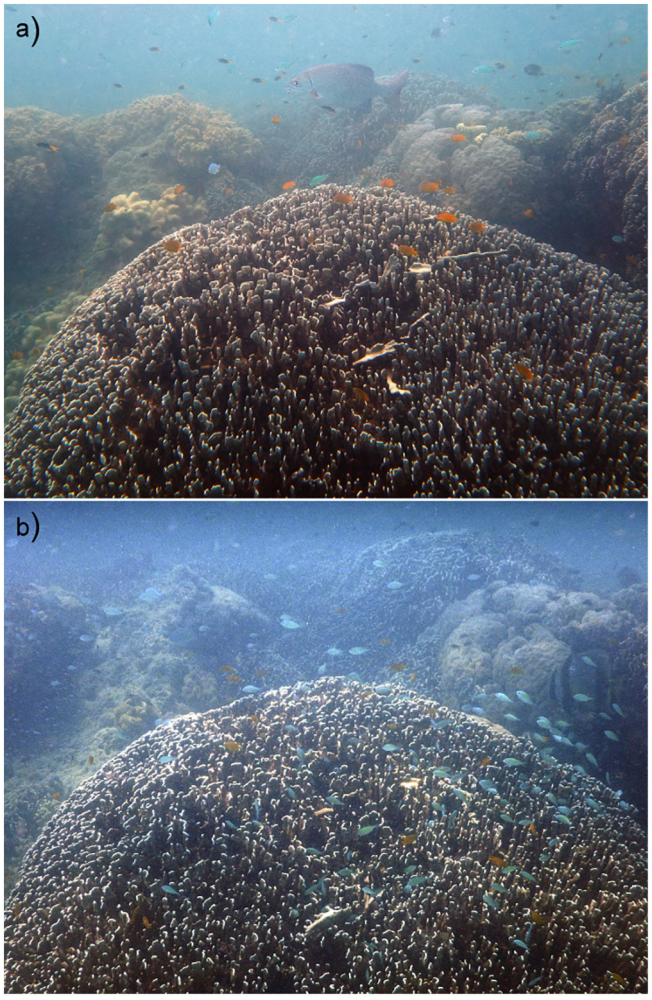

Fig. 7. A *Heliopora* coral colony photographed a) before (January 2016) and b) after (October 2016) mass bleaching, showing an increase in the abundance of *Chromis viridis* between sampling periods.

At a local, 1 m^2 scale, however, reef fishes exhibited a response to the presence of filamentous cyanobacteria that reflected their response to *Acropora* loss, with a strong spatial mismatch between the cover of cyanobacteria and local declines in fish abundance. Fish losses were not pronounced or concentrated in quadrats that experienced a proliferation of cyanobacteria. Conversely, some of these cyanobacterial-dominated quadrats even exhibited small increases in fish abundance. Again, our spatial matching methodology reveals interesting patterns that question traditional assumptions and highlights the need for caution when ascribing causality to observed patterns. Although, on average, our data agrees with previous studies, with a significant overall decrease in the abundance of reef fishes following coral loss and algal outbreaks, the patterns observed at a larger, 100 m^2 scale, do not translate to a local, 1 m^2 scale. Although undoubtedly linked, care must be taken when assuming coral loss and subsequent algal outbreaks have a direct causative relationship with fish decline. Our data show that there is no cross-scale conformity in coral-fish interactions nor a simple linear or proportional relationship between coral loss and fish declines at a quadrat level.

4.5. Delayed effects of habitat degradation

Although the short-term responses of adult reef fishes to mass coral bleaching were not as severe as expected, we recognize the potential for lag effects due to 1) a loss of structurally complex, three-dimensional habitat structure, 2) a decrease in physiological condition of fishes over time, and 3) recruitment-driven population declines due to a loss of live coral settlement habitat. Firstly, bleaching-induced coral mortality and the loss of structural complexity have differential effects on reef fish assemblages (Pratchett et al., 2008a). Coral mortality as a result of thermal stress does not compromise the underlying coral skeleton, and although covered in algae, it can still be utilized by reef fishes for shelter. Hence, short-term post-bleaching changes in the assemblages of reef fishes are often restricted to coral-dependent species (e.g. Riegl, 2002; Shibuno et al., 1999; Spalding and Jarvis, 2002). However, over time, dead coral skeletons are eroded by biological and physical agents. It is this loss of structural complexity that appears to have the strongest impact on reef fishes, with effects extending beyond coral-dependent species (e.g. Garpe et al., 2006; Graham et al., 2006, 2007; Jones et al., 2004; Wilson et al., 2008). Most branching corals (>80%) in our study maintained their physical structure 6 months post-bleaching, although some started to show signs of shortening (S.T. pers. obs.). Hence, structural complexity was generally preserved in the timeframe of our study, and the negative impact of decreased topographic complexity as a result of the recent mass bleaching event, remains to be seen.

Secondly, underlying changes in fish physiology may only manifest over time. For example, Pratchett et al. (2004) found no significant short-term changes in the abundance of the obligate corallivore *Chaetodon lunulatus*; however, post-bleaching fishes had a lower physiological condition. A follow-up study revealed that *C. lunulatus* did indeed decrease in abundance over time (Pratchett et al., 2006). Finally, habitat degradation may also negatively impact fish settlement and recruitment, with population effects only evident over time. Many reef fish species preferentially recruit to live coral (e.g. Coker et al., 2013; Jones et al., 2004), while dead, algal-covered corals are actively avoided (e.g. Feary et al., 2007). A significant decrease in suitable settlement environment may therefore prevent replenishment of coral-associated species. In this context, our study must be regarded as a short-term response of adult fishes. However, even across our temporal scale, the expected fish-coral association was not as strong as anticipated and these data open up interesting possibilities for the long-term future of these species.

4.6. Conclusion

In summary, our study provides a unique perspective on the short-term effects of mass bleaching on fish populations and reveals patterns that would go undetected using traditional sampling methodologies. Although we documented an overall decrease in both the abundance of resident reef fishes and the cover of live coral, in response to mass bleaching at Lizard Island, patterns at a local, 1 m^2 scale, were invariably spatially mismatched. Reef fishes were able to persist at degraded sites that were devoid of live coral and or inundated with cyanobacteria, while other sites exhibited considerable increases in post-bleaching fish abundance that are indicative of spatial movements. Furthermore, the effects of coral loss on obligate live coral-dwelling species were surprisingly limited, compared to the staggering losses of live *Acropora*. These results challenge commonly held assumptions regarding the tight link between live coral-dwelling damselfishes and habitat-forming *Acropora* corals. The relationship between fish loss and coral loss, therefore, appears to be a rather complex one, and care is needed when ascribing causality from observed patterns obtained from larger spatial scales. Our results offer a degree of optimism, albeit cautious, that fishes are far more behaviourally resilient than we may have previously assumed based on correlations at larger spatial scales.

Author contributions

DRB conceptualized the study. RS, ST, DRB collected the data; ST processed the images and analysed the data; SW wrote the first draft of the manuscript and created the figures; All authors developed the manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.09.114.

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